

A new probable stem lineage crustacean with three-dimensionally preserved soft parts from the Herefordshire (Silurian) Lagerstätte, UK

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A new arthropod with three-dimensionally preserved soft parts, *Tanazios dokeron*, is described from the Wenlock Series (Silurian) of Herefordshire, England, UK. Serial grinding, digital photographic and computer rendering techniques yielded ‘virtual fossils’ in the round for study. The body tagmata of *T. dokeron* comprise a head shield and a long trunk. The head shield bears six pairs of horn-like spines and the head bears five pairs of appendages. The antennule, antenna and mandible are all uniramous, and the mandible includes a gnathobasic coxa. Appendages four and five are biramous and similar to those of the trunk: each comprises a limb base with an endite, an enditic membrane, and two epipodites, plus an endopod and exopod. The hypostome bears a large cone-like projection centrally, and there may be a short labrum. The trunk has some 64 segments and at least 60 appendage pairs. A very small telson has the anus sited ventrally in its posterior part and also bears a caudal furca. Comparative morphological and cladistic analyses of *T. dokeron* indicate a crustacean affinity, with a probable position in the eucrustacean stem group. As such the epipodites in *T. dokeron* are the first recorded in a eucrustacean stem taxon. The new species is interpreted as a benthic or nekto-benthic scavenger.

Keywords: Arthropoda; Crustacea; exceptional preservation; Herefordshire Lagerstätte; Silurian; Wenlock Series

1. INTRODUCTION

The Herefordshire Lagerstätte from the Silurian Wenlock Series (approx. 425 Myr ago) of the Welsh Borderland (Briggs *et al.* 1996) represents one of only a few Lagerstätten known from the *ca* 70 Myr period between the Cambrian and the Devonian. This deposit has yielded radiolarians (Orr *et al.* 2002; Siveter *et al.* 2007a); a diversity of sponges; a polychaete worm (Sutton *et al.* 2001c); an aplousobranch-like mollusc (Sutton *et al.* 2001a, 2004); a platyceratid gastropod (Sutton *et al.* 2006); orthoconic nautiloids; several arthropods, including a pycnogonid (Siveter *et al.* 2004), a stem-group chelicerate (Orr *et al.* 2000b; Sutton *et al.* 2002), two myodocopid ostracodes (Siveter *et al.* 2003a, 2007b), a barnacle (Briggs *et al.* 2005) and a phyllocarid (Briggs *et al.* 2004); a brachiopod (Sutton *et al.* 2005b); several echinoderms, including an asteroid species (Sutton *et al.* 2005a); graptolites; and a number of organisms whose affinities remain enigmatic. The new species established here represents the fifth crustacean described from this Lagerstätte, the 78 known specimens comprising approximately 3% of the recorded fauna.

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2. MATERIAL AND METHODS

The fossils are preserved in three dimensions as calcitic void fills in early diagenetic carbonate concretions within volcanoclastic sediments (Orr *et al.* 2000a) and they retain fine morphological detail of external surfaces. Specimens were reconstructed through a combination of serial grinding, digital photography and computer rendering techniques, which produced three-dimensional ‘virtual fossils’ for study (Sutton *et al.* 2001a,b, 2002). Two specimens were reconstructed following serial grinding at 30 µm intervals: OUMNH C.29601 in entirety, OUMNH C.29602 anteriorly only. OUMNH C.29601 was cut prior to grinding with a 300 µm saw (twice anteriorly) and a 2 mm saw (posteriorly); these cuts are represented by gaps in the reconstruction. The virtual specimens were studied using interactive stereo-capable viewing software and hard-copy stereo-pair images.

3. SYSTEMATIC PALAEONTOLOGY

Phylum: Arthropoda

Subphylum: Crustacea

Genus: *Tanazios* gen. nov.

Derivation of name: Greek, *tanaos* (long) + *zoon* (animal) + *pelagios* (of the sea)

Diagnosis: Tagmata comprise a head shield and trunk. Head shield comprises axial and fringe areas, the latter bearing six pairs of horn-like spines. Head bears five pairs of

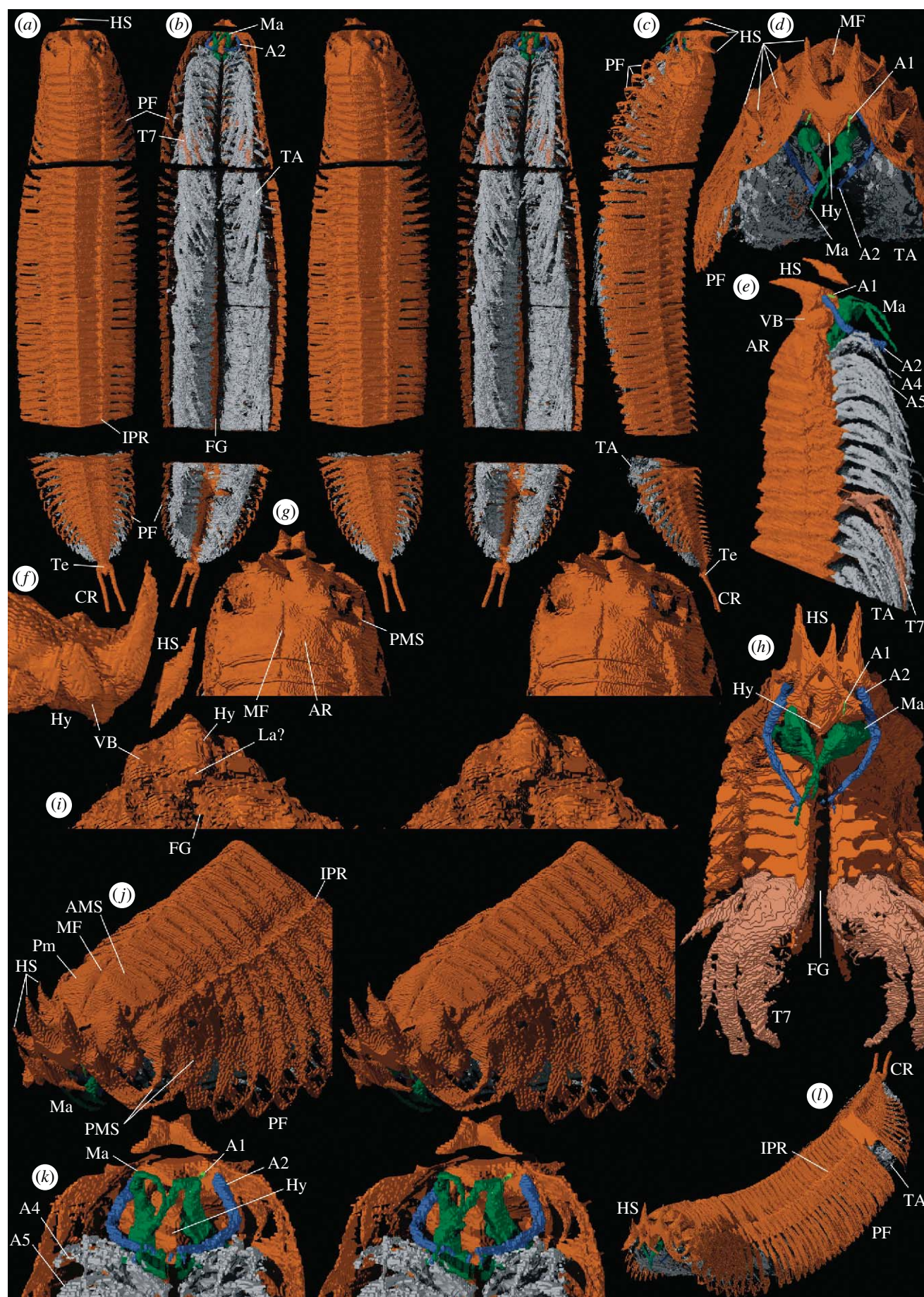


Figure 1. (Caption opposite.)

Figure 1. (*Opposite.*) *Tanazios dokeron*. (a–l) Holotype, almost complete specimen, OUMNH C.29601, ‘virtual’ reconstructions. (a–c,l) Dorsal and ventral stereo-pairs, lateral and anterolateral views, all $\times 4$. (d,h,j) Head region and anterior part of trunk, anterior tip of head shield removed, anterior view; head region and anterior part of trunk, lateral part of head shield, outer part of pleural region, and trunk appendages one to six removed, anteroventral view; head shield and anterior part of trunk, anterolateral stereo-pair; all $\times 10$. (e) Head region and anterior part of trunk, lateral part of head shield and outer pleural region removed, lateral view, $\times 9$. (f) Anterior part of head, head shield removed, lateral view, $\times 14$. (g) Head shield and anterior two trunk segments, dorsal stereo-pair, $\times 8$. (i) Head and anterior part of trunk regions, head shield and appendages removed, posteroventral stereo-pair, $\times 16$. (k) Head and anterior part of trunk regions, ventral stereo-pair, $\times 15$. Abbreviations used in figures 1–3: A1, appendage 1: antennule; A2, appendage 2: antenna; A4, appendage 4; A5, appendage 5; AH, artificially filled-in head shield; AMS, anterior margin of segment; An, anus; AO?, atrium oris ?; AR, axial region; Ba, basipod; Co, coxa; CR, caudal ramus/rami; DE, dorsal epipodite; DF, dorsal flap; Ed, endite; EM1–EM3, enditic membrane elements 1 (proximal)–3 (distal); EM, enditic membrane (undifferentiated); En, endopod; Ex, exopod; FR, Fringe region; FG, food groove; HHS, contact of head with ventral face of head shield; HS, horn-like spines; Hy, hypostome; HyS, hypostomal spine; IPR, inner pleural region; La?, labrum ?; LB, limb base; LM, lateral margin of hypostome; Ma, mandible: appendage 3; MF, median furrow; MHS, margin of head shield; Mo, mouth; Oe, oesophagus; PF, pleural facets; PMS, posterior margin(s) of segment(s); SA, swollen area; SP, subconical projection; T1–T4, trunk segments 1–4; T7, trunk appendage 7; TA, trunk appendages (undifferentiated); Te, telson; Tr, trunk; VE, ventral epipodite; VB, ventrolateral bulge of head; VF, ventral flap; WP, wing process.

appendages: tiny antennule, an antenna about five times longer and mandible, all uniramous, the mandible including a basis and a large coxa with a well-developed gnathobase; appendages four and five biramous, structurally the same as the trunk appendages. Hypostome with large, central cone-like projection. Trunk elongate, length-to-width ratio 4.5 : 1, comprising approximately 64 segments, each with one appendage pair except possibly segments 61–64. Trunk appendages each comprise limb base with an endite, enditic membrane and two epipodites, plus a slender endopod and exopod. Telson small, bearing two long caudal rami. Anus ventral near posterior of telson.

Species: *Tanazios dokeron* sp. nov

Derivation of name: Greek, *dodeka* (twelve) + *kerouchos* (horned) + *epikranon* (helmet).

Diagnosis: as for the genus (monotypic).

Holotype: OUMNH C.29601 (figures 1, 2c–q,s and 3a–d,e and f(pars)), an almost complete specimen; median length 29.7 mm; maximum width (at between 0.4 and 0.6 times the overall length) 6.6 mm.

Other material: OUMNH C.29602 (figures 2a,b,r and 3e and f(pars)) and 76 other specimens. Datasets and specimens are housed in the Oxford University Museum of Natural History (OUMNH).

(a) Head shield

The head shield (figures 1a,g,j, 2a,b,r and 3a,c) is subsemicircular in dorsal outline, the length approximately 0.75 times the width and 0.1 the total median length of the body, and divided into a fringe and an axial region. The lateral margins converge gradually anteriorly and then more abruptly to a transversely short anterior margin; posterolaterally they define a narrow, high projection with a gently rounded posterior margin. The posterior margin is subtransverse. In lateral outline, the head shield is wedge shaped, and in frontal view its anterior margin forms an inverted ‘v’, curving gently downwards and outwards (figure 2a). The anterolateral part of the fringe region bears an array of six pairs of variably sized, dorsally projecting, horn-like spines, including one pair on the anterior margin and the largest pair posterolateral of these.

The axial region is semi-ovoid in dorsal outline, defined anteriorly by a sagittally wide furrow which becomes narrower laterally, is convex transversely and sagittally and 2.3 times as wide as long, and divided by a narrow median furrow that extends weakly beyond it, just posterior to the largest spines. Lateral to the posterolateral

margin of the axial region, there is a narrow ledge that pinches out anteriorly and continues posteriorly as the inner pleural region of the trunk. Posteriorly in the axial region, a shallow transverse furrow defines the anterior margin of a segment similar in length to those of the trunk (seen especially on the left side; figures 1g,j and 3a,c). Laterally on the fringe region, there are traces of the posterior margins of possibly up to three pleurae; the most posterior of these is very weakly indicated and questionable, the two more anterior margins coincide with the two smallest spines. Eyes are absent.

(b) Head

The antennule lies beneath the largest spine, just lateral of the anterolateral margin of the hypostome (figures 1d,e,h,k, 2b, and 3e,f); it is uniramous and very short (individual podomeres are unresolved). The antenna (figures 1d,e,h,k, 2a,b,g and 3e,f), which inserts immediately posterolaterally of the antennule, is about five times longer, uniramous, subcircular in cross-section proximally, more ovoid distally, and includes three sections recognized by two angular changes in direction that are taken to represent podomere boundaries (the proximal section probably comprising two subequally long podomeres, the boundary between them recognized by slight marginal indentations in each ramus). A pair of short, widely diverging seta-like structures are present distally on the antenna of the holotype but they are absent on OUMNH C.29602 (figure 2a,b,r) and may be preservational artefacts. The mandible is separated from the antenna by much of the length of the hypostome, alongside the posterior part of which there is a ventrolateral bulge that lies beneath the third largest dorsal spine (figures 1f,i–k and 2o). The nature of this bulge is uncertain; it seems unlikely to represent an eye, as it is almost completely surrounded by the head shield and appendages.

The mandible is uniramous and comprises a presumed coxa (cf. figure 2h and, for e.g. Boxshall 2004, fig. 9f), basipod and endopod (figures 1d,e,h,k and 2h). The coxa is massive, subrectangular (the long axis transverse) and strongly gnathobasic. The gnathobase is distinguished from the coxa by a dorsal notch and raised sharply into an incisor-like process; its medial face is essentially planar and only slightly dentate. The basipod is subrectangular in cross-section, wide proximally, narrowing distally and curving medially. The first section (comprising one podomere?) of the endopod is slightly longer than the basipod and subovoid in cross-section; the second (one podomere) is



Figure 2. (*Caption opposite.*)

Figure 2. (*Opposite.*) *Tanazios dokeron*. (*a,b,r*) Partially reconstructed specimen, OUMNH C.29602; (*c–q,s*) holotype, almost complete specimen, OUMNH C.29601. (*a–r*) ‘Virtual’ reconstructions; (*s*) holotype specimen in rock. (*a,b,r*) Anterior part of head region, anterior and ventral stereo-pairs, lateral view, all $\times 15$. (*c–e*) Posterior part of trunk, the telson, and anterior part of caudal furca, dorsal, posteroventral and ventral stereo-pairs, $\times 18$, $\times 13$, $\times 18$. (*f*) Posterior part of trunk, the telson and caudal furca, posteroventral view, $\times 10$. (*g*) Antennae, anteroventral stereo-pair, $\times 13$. Dotted lines here and on (*h–j*) indicate discrete sections of the appendage defined by presumed podomere boundaries; some sections probably equate to one podomere, others to more than one (see description). (*h*) Mandibles, posteroventral stereo-pair, $\times 13$. (*i,j*) Third and fourth appendage pairs, posterodorsal stereo-pair, $\times 13$. (*k,q*) Seventh trunk appendage pair, posterodorsal and posterolateral stereo-pairs, $\times 13$, $\times 20$. The endopod is incomplete distally. (*l,o*) Head region and most anterior part of trunk, with and without short gut section, ventral stereo-pairs, $\times 14$. (*m,n,p*) Gut section, dorsal, ventral and lateral stereo-pairs, $\times 24$. (*s*) Transverse section through the trunk in the region of the base of second trunk appendage, $\times 12$.

approximately 0.25 times as long; the third (probably at least five short podomeres) is slightly longer than the first two combined and tapers to a finger-like distal extremity.

The fourth appendage comprises a limb base with an endite, enditic membrane and probably two epipodites, plus an endopod and exopod (figure 2*i*). The limb base viewed posteriorly is subrectangular in outline (long axis transverse) and bears a large, swollen, subtriangular area dorsomedially and a smaller one dorsolaterally (presumed muscle insertion sites). A dorsomedially to ventrolaterally elongate, flange-like endite projects posteromedially from the limb base; dorsally it is separated from the base by a notch and here its medial face is slightly faceted and aligned in the same plane as those of the mandibular gnathobase and the conjoined limb base endite and enditic membrane of each trunk appendage. The limb base bears an epipodite dorsally, and probably another more ventrally. Running from the medial side of the endopod at about mid-length to the posteromedian margin of the limb base, there is a fine membrane, details of which are obscure, but homologues on the fifth and the trunk appendages are clearer. The endopod is long, arises posteromedially from the limb base, is ribbon-like proximally as it trends ventroposteriorly, and becomes more finger-like distally; it appears to consist of three sections, the two most proximal (each one podomere?) of subequal length and the other most distal (in which podomeres cannot be distinguished) about twice as long as each of these. The exopod originates posterolaterally on the limb base, is ribbon-like, has a similar disposition to the endopod and probably also comprises three sections (thus at least three podomeres), and although imperfectly preserved distally, it is shorter.

The fifth appendage (figure 2*j*) is similar to the fourth but slightly larger; the enditic membrane projects more dorsally above the endite; and both ventral and dorsal epipodites are clearly present.

The hypostome (e.g. *sensu* Waloszek 2003) is sub-rectangular in overall outline, approximately 1.4 times as long as wide, and extends from just anterior of the antennules to the mandibular gnathobases (figures 1*d,f,h,i,k*, 2*a,b,l,o* and 3*e,f*). Its anterior margin is poorly resolved but appears to be transversely directed and to bear four small spines. Anterolaterally there is a relatively small, laterally projecting, wing-like process. In its anterior quarter, the hypostome projects ventrally and steeply backwards and inwards from the anterior and lateral margins, respectively, to a break in slope on which, bilaterally, there is a short spine. Posteriorly from here, the central body extends more ventrally to a cone-like central projection that extends posteriorly to approximately 0.6 of the hypostomal length. In its posterior

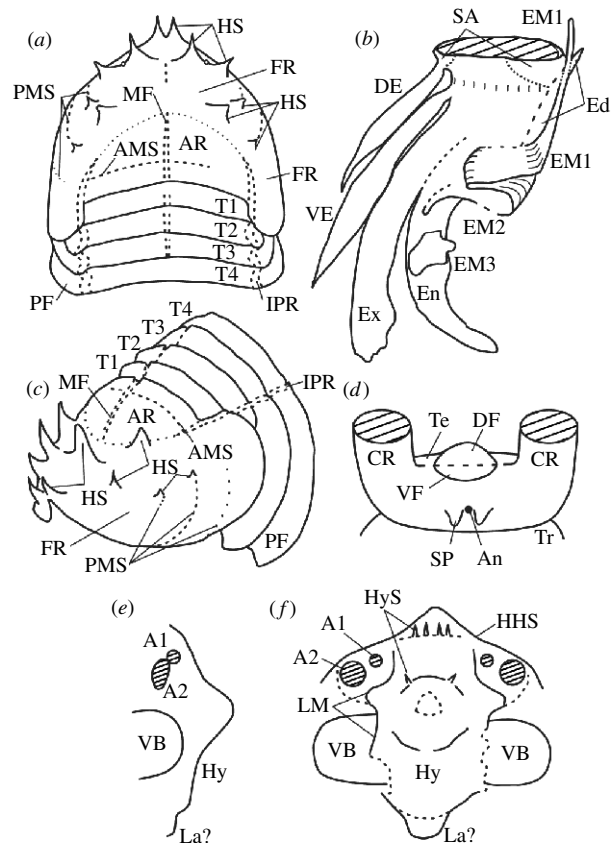


Figure 3. *Tanazios dokeron*. Interpretations of morphology, based on computer reconstructions of OUM C.29601 (holotype) and OUM C.29602. (*a,c*) Head shield and anterior four trunk segments, dorsal and anterolateral views, $\times 8$. (*b*) Seventh trunk appendage, posterodorsal view, $\times 15$. The endopod is incomplete distally. (*d*) Telson and part of caudal furca, posteroventral view, $\times 32$. (*e,f*) Hypostome and surrounding area, lateral and ventral views, $\times 18$. Diagonal hatches on *b* and *d–f* indicate sliced surfaces.

one-third, the hypostome descends ventrally and inwards steeply, and very steeply, from the lateral and posterior margins, respectively. The lateral margin is slightly convex medially and impinged on by the lateral bulge of the head. The presumed posterior margin is weakly convex posteriorly, posterior to which there is a short lip-like feature that may represent a labrum.

Dorsal to the hypostome and labrum there is a short, sediment-infilled gut section that is constricted where they meet (figure 2*l–n,p*). Immediately posterior to the constriction, this infill shows a pair of short ventrolateral projections, and dorsally it is roof-like; anterior to it the ventral surface is subplanar, and the dorsal surface irregular. The constriction is interpreted as the mouth, the sediment posterior to it as possibly infilling an atrium

oris, and that anterior to it as infilling the beginning of the oesophagus; whether the other more minor structures reflect biological or diagenetic features is uncertain.

(c) *Trunk*

The trunk of the holotype is made up of approximately 64 segments inclusive of a tiny terminal axial piece, plus a telson and caudal furca (figure 1*a–c*). One anterior segment and five posterior segments are inferred to have been present in the two gaps that represent saw cuts. Segments are mostly similar in size; the anterior approximately 10 become progressively smaller anteriorly and the posterior approximately 20 smaller posteriorly, the last few segments becoming tiny. All trunk segments bear a single pair of biramous appendages with the possible exception of the last four (? perhaps too small to be preserved). A narrow deep food groove runs the length of the trunk, broadening somewhat posteriorly.

The axis is at least 0.8 times the width of the trunk across the inner pleural regions. A narrow median furrow continues from the head shield onto the first three segments. The axis is mostly roof-like in transverse profile, its sides sloping uniformly and progressively more steeply up to at least trunk segment 37. Approximately between segments 44 and 55, the central part of the axis descends very steeply laterally and the outer part more gently. Posterior to segment 55, the steeper central axial part progressively takes up the whole of the axial width. In lateral view, the anterior segments have a posteriorly directed, saw-toothed dorsal outline; from about segment 22, the apex of each is transformed into a medial spine except for the two segments immediately anterior to the terminal piece (figure 2*c*), which each bear a small median node.

The pleural region comprises a very narrow inner ledge and, except for the first segment, descending pleural facets (figure 1*j*). The first segment lacks a pleura, which may have been incorporated into the posterolateral part of the head shield. The second pleura is reduced in size relative to more posterior pleurae. The pleural facets have a subrounded-to-pointed distal margin, a slightly thickened posterior margin and they show slight (15–20%) overlap. In lateral view, the anterior facets swing forwards, the mid-trunk ones point downwards and the posterior ones swing progressively backwards; these attitudes may in part be controlled by the dorsal (concave) curvature of the trunk. The last three or four trunk segments either lack pleurae or they are too small to be preserved or resolved. Immediately posteroventral of the posterior axial margin of many segments, there is a subparallel line that may represent the posterior margin of an articulating half-ring (figure 1*g,j*).

The trunk appendages vary in size proportional to their respective segments. The structure of each appendage is the same and is like that of head appendages four and five, although the smaller posterior ones are less well resolved. The seventh trunk appendage (individually rendered; figures 1*h*, 2*k,q* and 3*b*) shows that the limb base is convex anteriorly in lateral view, and subrectangular in outline (long axis dorsoventral) and weakly divided into dorsal and ventral parts along the line of curvature in posterior view. The limb base has a large, swollen (presumed muscle attachment) area dorsomedially and a smaller one dorsolaterally, and a well-developed dorsomedially to ventrolaterally elongate, posteromedially directed flange-like endite. The more dorsal

of the two large, blade-like epipodites is the smaller. Both are variously disposed backwards and outwards and are apparently articulated basally.

There is an enditic membrane comprising three separately attached flap-like elements two of which (at least) are united. The first element is attached to the limb base where the base is met by the medial margin of the endopod; it is horizontally disposed and medially turns upwards into a curtain-like section that becomes partially confluent with the endite, which in some appendages is seen to project dorsomedially through it. The second originates on the endopod proximally, at the bottom of its downward curve and at its mid-width; it extends medially, then folds dorsally and extends laterally before folding dorsally again to become confluent with the first element. The third element connects to the endopod just distal of where the ventroposterior curve of the endopod levels out, and at its mid-width, distal to which it is raised slightly off the endopod, though otherwise its form is unresolved.

The seventh trunk endopod curves ventroposteriorly proximally where it is broad, flat and ribbon-like; distally it becomes very much narrower, more subovoid in cross-section and trends posteromedially, but is here incomplete (when entire, the trunk endopods extend much more distally in finger-like form (figure 1*b*), as in head appendages four and five). If the distal two flaps are proxies for podomere boundaries, at least three podomeres are present. The exopod is shorter than the endopod and slightly less broad than it is proximally where (as with head appendages four and five) they touch, though it is unknown whether their margins here are fused; it is ribbon-like, curves ventroposteriorly, narrowing only slightly as it does so, and ends in a short, broadly pointed termination. Exopod podomere boundaries cannot be determined.

(d) *Telson and caudal furca*

Behind the terminal axial piece, there is a small telson that bulges laterally and is extended posteriorly into a short, median, triangular flap beneath which is a similar ventral flap (figures 2*c–f* and 3*d*). Two incomplete ovoid (long axis horizontal) rami, with a preserved length 0.08 times the body length, project from the posterolateral margins of the telson to form a caudal furca; proximally they are subparallel, distally they deflect weakly outwards (figure 1*a–c*), and they lack evidence of podomeres. A small orifice sited ventrally in the posterior part of the telson is interpreted as the anus; it is flanked by a pair of short, posteroventrally directed subconical projections.

4. DISCUSSION

(a) *Affinities*

The gross morphology of *Tanazios*—a long, narrow body with only two tagmata, and a trunk with numerous segments each bearing a pair of homonomous biramous appendages—resembles that of extant and fossil remipedes (Schram *et al.* 1986; Emerson & Schram 1991), and also the purported stem crustacean *Ercaia minuscula* from the Lower Cambrian of Chengjiang (Chen *et al.* 2001). However, this type of morphology is probably plesiomorphic (cf. the ‘urcrustacean’ proposed by Hessler & Newman 1975), and moreover all of these taxa differ in detail. *Tanazios* also shows resemblance in overall body form to the Hunsrück Slate (Devonian) monotypic arthropods *Eschenbachiellus*,

Cambronatus and particularly *Wingertshellicus* (Briggs & Bartels 2001; Moore *et al.* in press), which were described as 'crustaceanomorphs'. However, Boxshall (2004) regarded the crustacean affinities of *Cambronatus* as equivocal, and *Cambronatus* and *Wingertshellicus* have been allied tentatively (Haas *et al.* 2003) with the monotypic Hunsrück Slate genus *Devonohexapodus*, as hexapods within Atelocerata (myriapods + hexapods), but the hexapod affinities of *Devonohexapodus* have been disputed (Regier *et al.* 2004; Willman 2005). The body of *Tanazios* is generally myriapod-like, and if the long, apodous area of the head between the mandible and the preceding appendage were to represent the intercalary segment of that group, a stem mandibulate assignment for it could be entertained. Under this scenario, the two rami recognized herein as the antennule and antenna would then represent an antennule that comprised two branches, one or both of which is a flagellum (Boxshall 2004). However, while these two rami are proximally close, they show no sign of joining, a common origin, or being branches of the same appendage, and neither ramus seems particularly flagellum like.

The morphology and arrangement of the head appendages in *Tanazios*, together with the morphology of the trunk appendages, indicate that its affinities lie with the crustaceans. This is supported by our cladistic analysis of the morphological character matrix of Wills *et al.* (1998), to which we added *Tanazios*. Although the phylogenetic conclusions of Wills *et al.* (1998) have been superseded by more recent molecular and total evidence approaches (e.g. Giribet *et al.* 2001, 2005; Regier *et al.* 2005; Mallatt & Giribet 2006), and by re-evaluation of the position of Trilobita (Scholtz & Edgecombe 2005), it remains the most recently published morphological database that accommodates both palaeontological and neontological characters, and hence still provides a basis for the placement of fossils within the major arthropod groups. Having determined a crustacean affinity for *Tanazios*, we analysed its placement within the more comprehensive morphological database of fossil and living crustaceans provided by Wills (1998), which includes nearly three times as many relevant taxa. *Tanazios* falls in a basal position, more derived only than the Cambrian *Odaraia*. (Note, however, that recent molecular phylogenies suggest that remipedes, used as outgroup by Wills (1998), are not basal crustaceans.)

We then considered the placement of *Tanazios* within the crustacean stem group using the phylogenetic scheme put forward by Waloszek and co-authors (Waloszek & Müller 1990, 1998; Waloszek & Szaniawski 1991; Waloszek 1999; Waloszek 2003). The presence in *Tanazios* of a short antennule with few podomeres identifies it as a total group (stem plus crown) crustacean. Special distal setae used for locomotion and feeding on the antennule, a moveable proximal endite and exopodal setae directed towards the endopod in the postantennular limbs, are apparently lacking in *Tanazios*, and other autapomorphies of the total group crustaceans concerning endopod and exopod podomere numbers cannot be determined. The presence of a mandible with coxa, five limb-bearing head segments, and a labrum and atrium oris, suggest a placement for *Tanazios* within the labrophoran clade (Phosphatocopina + Eucrustacea; Siveter *et al.* 2003b). However, in *Tanazios*, the morphology of the basal part of the antenna appears simple, presumably reflecting an undifferentiated limb base, and thus it seems to lack a coxa

(*sensu* Waloszek), the presence of which is an autapomorphy of Labrophora; the possible small labrum and atrium oris might simply represent a posterior extension of the hypostome and associated gut; furthermore, a head with five limbs is known from less derived, labrophoran stem lineage derivatives such as *Henningsmoenicaris*, *Oelandocaris* and, though possibly not fully so, *Martinsonia*. Other labrophoran autapomorphies (Siveter *et al.* 2003b; Waloszek 2003) are indeterminate in *Tanazios* (fusion of antennal to maxillary sternites into a single sternum), or are apparently absent (paragnath outgrowths on the mandibular sternites/part of the sternum, and fine hairs on the sides of the labrum). Key phosphatocopine autapomorphies, such as a phosphatic, bivalved head shield enclosing the body and reduction of trunk segments to less than six, are also absent. The final autapomorphy listed for Phosphatocopina, an antennule much reduced in size and numbers of podomeres and setae, can mostly be confirmed in *Tanazios*. *Tanazios* lacks key eucrustacean autapomorphies, such as modification of the fourth head appendage into a specialized mouthpart and the presence of a terminally positioned anus. There is slight faceting on the dorsomedial part of the endite of the fourth, and to a lesser extent fifth, appendage of *Tanazios* (see description), but these limbs are essentially like those of the trunk (even in Cephalocarida, which is often referred to as showing the least serial specialization of limbs among Eucrustacea, the fourth (adult) limb is more differentiated from the fifth and the trunk limbs; see Hessler 1969). A caudal furca, articulated and leaf shaped with marginal setation, may be an autapomorphy of Eucrustacea, but possible furcae have also been identified in Phosphatocopina, so potentially moving this character down to this level (Maas *et al.* 2003; Waloszek 2003).

Thus, *Tanazios* appears to fall within the eucrustacean stem lineage in the scheme of Waloszek and co-authors, either basally within (a redefined) Labrophora, or with the stem-lineage derivative forms *Cambropachycope*, *Goticaris*, *Cambrocaris*, *Martinsonia*, *Henningsmoenicaris* and *Oelandocaris*, outside the labrophoran clade. Relationships among the stem-lineage derivatives remain unresolved apart from the sister group relationship of *Cambropachycope* and *Goticaris* (Cambropachycopidae), and most recently *Oelandocaris* has been considered the most basal of them (Stein *et al.* 2005). *Tanazios* differs from these other taxa in possessing a mandible with a coxa, and on the evidence of this character, it would be considered the most derived of them (see Waloszek & Müller 1990; Waloszek 2003; Stein *et al.* 2005; though see also Waloszek & Szaniawski 1991 for a report of a coxa in *Cambrocaris*). The uniramous mandible and antenna of *Tanazios*, both presumably representing the derived condition, are also unique among these genera, and the overall form of its post-mandibular appendages is distinct, in particular the slender, apparently setae-less exopod and epipodite-bearing limb base.

Tanazios is the first of the five crustaceans described from the Herefordshire Lagerstätte that does not appear to belong to the crown group. The recognition of epipodites in a probable eucrustacean stem-group form is noteworthy; these structures are otherwise known only from undoubted eucrustaceans, the Herefordshire Lagerstätte *Colymbosathon*, *Cinerocaris* and *Nymphatolina* representing the earliest examples. Given the mounting evidence of a close hexapod–crustacean relationship (e.g. Giribet *et al.* 2005;

Regier *et al.* 2005), this provides evidence that 'structural progenitors' of insect wings (Averof & Cohen 1997) may have existed in the earliest crustaceans (Boxshall 2004).

(b) *Mode of life*

The Herefordshire Lagerstätte was deposited in an outer shelf muddy bottom setting within the Anglo-Welsh Basin under maximum water depths of approximately 200 m (Briggs *et al.* 1996). *Tanazios* does not have a typical arthropod 'walking' leg. However, its apparent blindness is more consistent with living on or near the bottom than primarily in the water column; other co-occurring, presumed benthic taxa were blind (e.g. the chelicerate *Offacolus*, the polychaete *Kenostrychus* and the vermiform mollusc *Acaenoplax*), while natatory forms (the ostracodes *Colymbosathon* and *Nymphatolina*, and the phyllocarid *Cinerocaris*) possessed eyes. The numerous trunk appendages of *Tanazios* would probably have enabled active swimming, the caudal furca functioning as a stabilizer. The epipodites, by analogy with living crustaceans, would have served in respiration, either directly or to ventilate other respiratory parts—perhaps the exopods, the body wall or maybe even the enditic membranes. Anterior transportation of food along the endite-flanked food groove (the plesiomorphic state for euarthropods; Hessler & Newman 1975; Waloszek 2003) must have occurred, and the enditic membranes may have helped contain it in this channel. The similarity of the fourth and fifth head appendages to those of the trunk implies similarity of function. The tiny antennule is not of typical sensorial form, at least not mechanosensory, and it seems unsuited either for locomotion or food collection (Waloszek 2003; Boxshall 2004). Dorsoventral flexure of the trunk was probably possible to some degree: witness the overlap of pleural facets and the possible articulating half-rings. The horn-like dorsal spines may have been defensive.

Tanazios was blind and therefore probably not a predator, yet it had a substantial mandibular gnathobase; this suggests that it fed on detritus. *Tanazios* is thus interpreted as a benthic or nektobenthic scavenger.

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NOTICE OF CORRECTION

Figures 1 and 2, and the legend of figure 3 are now presented in the correct form.

8 August 2007